

Porphyra drewiana, a new species of red algae (Bangiales, Rhodophyta) from Brazil

Javier Coll¹ and Eurico C. Oliveira^{2*}

¹Departamento de Botânica, Facultad de Química, Universidad de la Rep. O. del Uruguay, CC 1157, CP 11800 Montevideo, Uruguay and ²Instituto de Biociências, Universidade de São Paulo, C. postal 11461, 05422–970 São Paulo, SP, Brazil

SUMMARY

Porphyra drewiana Coll et Oliveira, sp. nov., is described from plants collected on the south-east coast of Brazil. The species proposed is monostromatic, monoecious, monoplastidial, without marginal microscopic teeth and does not produce monospores. Both phases, leafy and filamentous, have three chromosomes. Morphologically the most similar species is *Porphyra spiralis* Oliveira et Coll var. *amplifolia* Oliveira et Coll, from which it differs by: (i) thallus gross morphology; (ii) scattered pluristromatic areas of vegetative cells; (iii) division of the plastids prior to the nucleus at the first division of the carpospores mother cell; (iv) the number of carpospores and spermatia produced per mother cell; and (v) morphology and behavior of the filamentous phase in cultures. An identification key for the species referred to Brazil is included.

Key words: Bangiales, Brazil, chromosome number, *Porphyra drewiana* sp. nov., Rhodophyta.

INTRODUCTION

As the most economically important genus among the algae (Radmer 1996), *Porphyra* has been the target of a large number of publications on all aspects, including taxonomy (e.g. Oliveira and Coll 1975; Coll and Oliveira 1976; Coll and Cox 1977; Kapraun and Freshwater 1987, 1992b, 1993; Lindstrom and Cole 1992a; Dutcher and Kapraun 1994; Kornmann 1994; Broom *et al.* 1999). A recent review by Yoshida *et al.* (1997) indicated that the genus had 133 described species at that time. Nevertheless, its taxonomy is far from clear, and *Porphyra* species identification remains a problem (Coll and Oliveira 1977a; Lindstrom and Cole 1992c; Lindstrom 1993; Stiller and Waaland 1993; Yoshida 1997; Knight and Nelson 1999). The taxonomic problems are certainly aggravated by the fact that the genus is recognized to be paraphyletic (Oliveira *et al.* 1995; Müller *et al.* 1998).

In a revision of the taxonomy of Brazilian species, Oliveira and Coll (1975) concluded that none of the taxa previously referred to Brazil up to then could be accepted. Instead they described two new species with two varieties each, namely *Porphyra acanthophora* Oliveira et Coll var. *acanthophora* and *Porphyra acanthophora* var. *brasiliensis* Oliveira et Coll; and *Porphyra spiralis* Oliveira et Coll var. *spiralis* and *Porphyra spiralis* var. *amplifolia* Oliveira et Coll. Yoneshigue (1985) found, in an upwelling zone, three other species previously referred to Uruguay: *Porphyra leucosticta* Thuret in Le Jolis, *Porphyra pujalsii* Coll et Oliveira and *Porphyra rizzini* Coll et Oliveira (Coll and Oliveira 1976, 1999).

Here we deal with some specimens that Oliveira and Coll (1975) could not assign to any of the recognized species because of insufficient material. Since then, extensive collections from southern and south-eastern Brazil have revealed that we were dealing with a distinct taxon, which is here proposed as a new species.

MATERIALS AND METHODS

The observations were made on live, formalin-preserved, and herbarium specimens. We also had access to *in vitro* cultivated material of both leafy and filamentous phases, held independently by M. Oliveira and E. Mizuno from the University of São Paulo. The type and additional specimens are deposited at the Herbarium of the Institute of Biociências, Universidade de São Paulo, Brazil (SPF). Hand sections were stained with aniline blue acidified with 1N HCl and mounted in Karo® syrup. Chromosome counts were made using hematoxylin, following the methodology described in Coll and Oliveira (1977a) for fresh material and Coll and Oliveira (1977b) for dried herbarium specimens.

*To whom correspondence should be addressed.

Email: euricodo@usp.br

Communicating editor: K. W. Nam.

Received 26 March 2000; accepted 25 October 2000.

RESULTS AND DISCUSSION

Diagnosis

Porphyra drewiana Coll et Oliveira sp. nov.

Plantae monoicae, monostromaticae, cellulis plasto unico stellato continentibus; laminae margine integrae sive dentibus microscopicis ornatis; isolatae vel 2–5 aggregatae; frondes violaceae, orbiculares, obovatae aut lanceolatae, ad 14 cm altae et 14 cm latae usque, 25–45 µm crassitudine in medio, textura membranaceae, delicatae, siccitate chartae haud adherentes. Carpospora cum spermatiis primo intuitu confusa, in macula minutas disposita, microscopica, prope margines; carpospora 8 (–16) pro sporangio, in 2 stratis ordinata; spermatia 16 pro sporangio, in 4 stratis ordinata. Monosporae atque aplanosporae desunt. Super saxa in parte superiore litoris vulgo vigentes.

Plants monostromatic, typically with one entire blade (Fig. 1), rarely with deep lobes or a few blades (Fig. 2); attachment by a distinct discoidal holdfast; blades orbiculate, oblong, obovate or broadly lanceolate, umbilicate or cordate, up to 14 cm long; color deeply violet when alive; texture membranaceous, delicate, not rubbery or cartilaginous; not firmly adherent to paper on drying, then papery and breakable. Infertile margin entire, slightly undulated, without microscopic teeth (Fig. 3). Vegetative cells with one stellate plastid and a central pyrenoid, oval to polygonal, 10–12 µm in surface view (Fig. 3); total thickness of the blades, at the vegetative central portion, 25–45 µm; fertile pluristromatic portions are about 10–15 µm thicker. Small, elongate, irregularly distributed patches (50–150 µm) call attention to vegetative portions of the blade. In cross section these patches are formed by periclinal divisions of the vegetative cells, resulting in locally bi-pluristromatic areas, 2–3 times thicker than the rest of the thallus (Figs 4,5). Monospores (type II *sensu* Drew 1954, 1956), neutral spores (*sensu* Kurogi 1961) or aplanospores (*sensu* Conway *et al.* 1975; Piriz 1981) were never found. Spermatangia and carposporangia are intermixed (Figs 7,8) in a marginal–submarginal rosy band, which is almost continuous around the blade, which becomes perforated and eroded after spermatia and carpospores are shed (Fig. 1). The first division of the carpospores and the spermatia mother cell is periclinal (Fig. 6). The plastid divides before the nucleus in the first division of the carpospore mother cell, remaining in a central position between the two daughter plastids (Figs 9,10). Eight to 16 carpospores in two tiers and 16 spermatia in four tiers are produced per mother cell. Three chromosomes were counted in the nuclear divisions leading to spermatium formation (Fig. 11). At the type locality the leafy phase was collected on rocks at the upper intertidal fringe, in eutrophic waters at moderate wave-exposed sites, from May to December, being fertile after July.

Holotypus: SPF 53750, E. C. Oliveira *collegit*, 4.xii.1987, *in litore maris* Ilha do Boi, Vitória, Espírito Santo State, Brazil.

Etymology: Species named in honor of the late Professor Kathleen M. Drew for her outstanding contributions to the knowledge of *Porphyra* and related genera.

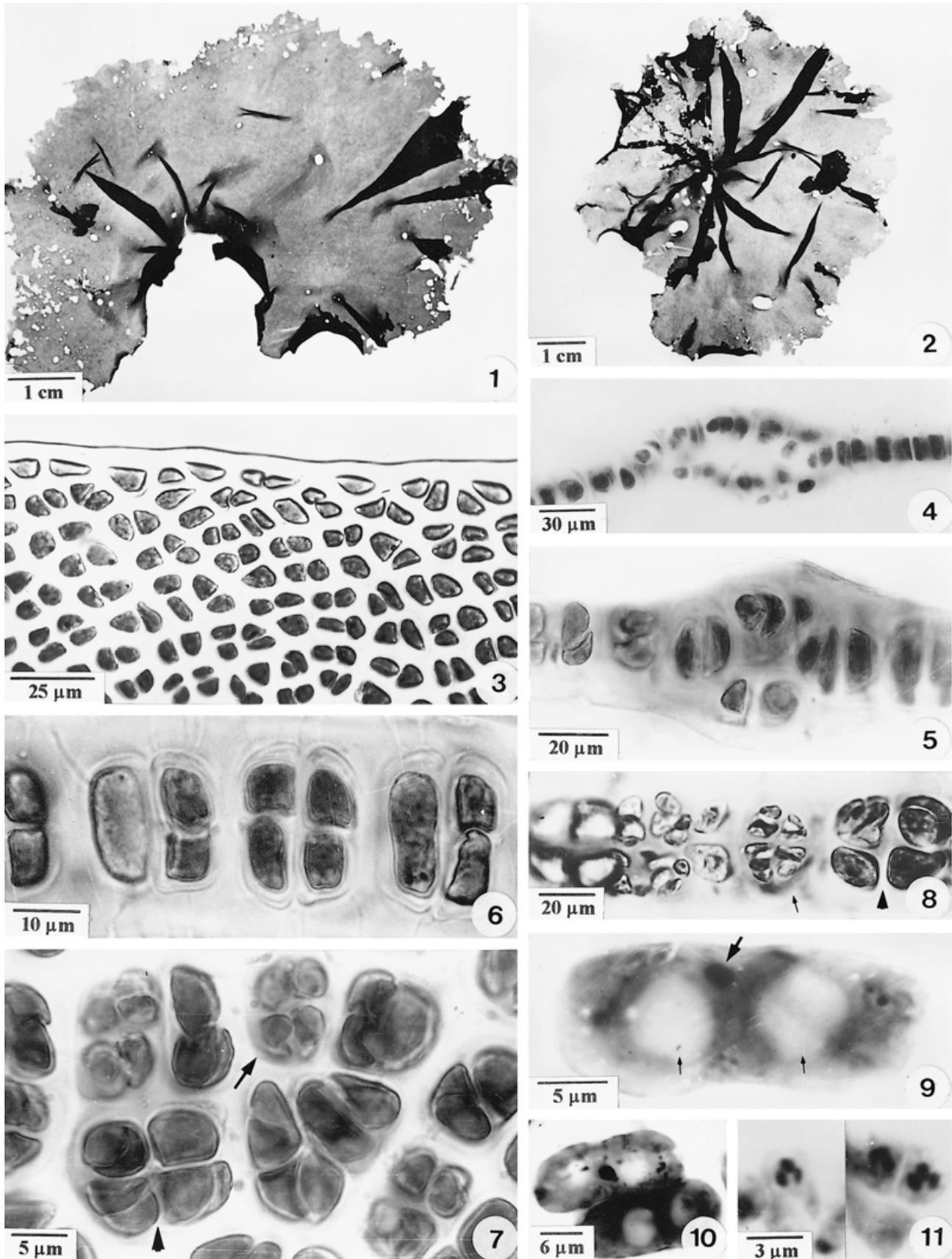
Representative specimens: SPF 889, coll. at Caiobá, PR, by A. Joly, 4.xi.1950; SPF 905, coll. at Passagem, Guaratuba, PR, by A. Joly, 13.ii.1951; SPF 1269, coll. at Matinhos, PR, by Y. Ugadim, 5.ix.1968; SPF 1298, coll. at Ilha do Farol, PR, by Y. Ugadim, 5.ix.1968; SPF 1298, coll. Ilha do Mel, PR, by Y. Ugadim 5.ix.1968; SPF 55994, coll. Ilha do Boi, Vitória, ES, by E. Oliveira 21.x.1998.

As we could not demonstrate the occurrence of fecundation we opted to use the traditional nomenclature for reproductive cells instead of the more recent one recommended by Guiry (1990). We also preferred the more descriptive term monospore instead of archeospore (Magne 1991).

The unusual periclinal division of the vegetative cells, forming small pluristromatic patches may be unique to this species. However, a similar situation was reported for *Porphyra capensis* Kützing, type locality Cape Town, South Africa (Kützing 1843; J. Agardh 1882; Hamel 1928). Three other species: *Porphyra gardneri* (Smith et Hollenberg) Hawkes, *Porphyra saldanhae* Stegenga, Bolton et Anderson and *Porphyra* sp. are also known from that region. However, these species do not have the pluristromatic patches and are clearly different from *P. drewiana*. Besides, *P. capensis* and *P. saldanhae* have cells with two chloroplasts, *P. gardneri* has a narrow, linear thallus and the indetermined species has a different distribution of reproductive cells (Stegenga *et al.* 1997).

The division of plastids prior to nuclear division and their migration to the poles of the carpospore mother cell in *P. drewiana* were also reported for *Porphyra pujalsiae* Coll et Oliveira (as *P. pujalsii* nom. nud. in Coll and Oliveira 1976). Dangeard (1927) clearly described and illustrated a similar occurrence in *Porphyra linearis* Greville [as *Porphyra umbilicalis* f. *linearis* (Greville) Rosenvinge] during the first division of what he assumed to be fertilized carpogonia. However, he did not note this in what he considered to be unfertilized carpogonia. Lindstrom and Cole (1992c) reported on the frequent occurrence of two chloroplasts in cells of *Porphyra lanceolata* (Setchell et Hus in Hus) G.M. Smith in G.M. Smith and Hollenberg apparently due to a division of the chloroplast prior to cell division. However, they do not say if the chloroplast divides before or after the nuclear division.

In some preparations, vestiges of what could be fecundation channels can be seen on the mucilage above carposporangia (Fig. 6). However, the presence of



Figs 1–11. *Porphyra drewiana* sp. nov. 1. Holotype. 2. Isotype. 3. Detail of the infertile margin. 4,5. Cross section of vegetative polystromatic areas. 6. Cross section showing the first periclinal division of fertile cells. 7. Early stages in the formation of carpospores (arrow head) and spermatia (arrow), side by side, in surface view. 8. Cross section of a fertile portion showing carpospores (arrow head) and spermatia formation (arrow). 9,10. Carpogonium cell showing two chloroplasts (small arrows) and one nucleus (large arrow). 11. Spermatia with three late-prophase chromosomes.

Table 1. Comparison between the leafy phases of *Porphyra spiralis* var. *amplifolia* and *Porphyra drewiana*

	<i>Porphyra spiralis</i> var. <i>amplifolia</i>	<i>Porphyra drewiana</i>
Habit	Tufted	Not tufted
Blade length/width	Always > 2	Ca. 1
Blade thickness (μm)		
Vegetative	20–25	25–45
Reproductive	30–35	40–60
Base	Not cordate	Cordate
Holdfast	Unconspicuous	Discoidal
Carpospores per carposporangia	16 (–32) in 2 (–4) tiers	8 (–16) in 2 tiers
Spermatia per spermatangia	64 in 4 (–8) tiers	16 in 4 tiers
Bi-pluristromatic patches	Absent	Present
Plastid division	After nuclear division	Before nuclear division
Carpogonial cell		
height/width ratio	maximum 1.5	2.0

three chromosomes, both in spermatia and carpospores and also in the filamentous phase, obtained in culture suggests that carpospores are produced by unfertilized carpogonia (J. Coll and E. C. Oliveira, unpubl. data). Cole (1990) should be seen for an extended discussion on the place of meiosis in the life histories of different species of *Porphyra*, which could occur on the fertilized carpogonium, conchospore formation or conchospore germination. The absence of alternation of ploidy between the leaf and filamentous phases was also remarked by Kapraun and Freshwater (1987) for southerly North American species of *Porphyra*.

As remarked before, *P. drewiana* has some similarities with *P. spiralis* var. *amplifolia*. However, the assemblage of dissimilarities between them, as shown in Table 1, in addition to the size of chromosomes [larger in the new species (J. Coll and E. C. Oliveira, unpubl. data)] points toward the recognition of *P. drewiana* as a new taxon. This is also supported by data from Oliveira (1993) who has shown that the filamentous phase of *P. drewiana* (as *P. drewiae* Coll et Oliveira, *nom. nud.*) behaves differently in culture to *P. spiralis* or *P. acanthophora* with regard to temperature, and they are a distinctive shade of red. In addition, Mizuno (1998) showed that *P. drewiana* (as *P. drewiae*) can very easily be induced to produce conchosporangia *in vitro*, which is not the case with the other Brazilian species.

The large number of endemic species that have been described for this genus (e.g. Broom *et al.* 1999; Knight and Nelson 1999) could be an indication of a high speciation rate, but could also just be a consequence of the lack of reliable characters to identify species. One could also speculate that this high rate of endemism could be related to: (i) the fact that growth and reproduction of filamentous and leaf phases are triggered by different and specific combination of environmental factors (e.g. Nam-Gil 1999); (ii) population isolation due to limited dispersion or low viability of spores; or (iii) the peculiarities of life history. However, this situation could change in the near future

as the traditional approach of utilizing morphological characters of the leafy phase for species identification is complemented by gene sequencing.

ACKNOWLEDGEMENTS

We acknowledge Emeritus Professor Kathleen M. Cole for a thoughtful revision of an earlier version of the manuscript, and Professor Paul C. Silva for valuable suggestions on nomenclature. We also acknowledge Dr Edison J. de Paula for fruitful discussions about the biology and culture of *Porphyra* and for his cooperation during the Postdoctoral research of JC at the Algal Culture Laboratory of the University of S. Paulo (Brazil). This research was partly supported by CNPq (National Research Council) and FAPESP (São Paulo's State Research Foundation) to E. C. O. (Brazil), and CSIC (University of Uruguay Scientific Commission) to J. C. (Uruguay).

REFERENCES

- Agardh, J. G. 1882. Till Algernes Systematics. Afd. 3. VI. Ulvaceae. *Lund Univ. Arsskr.* **19**: 1–177. Lund.
- Broom, J. E., Jones, W. A., Hill, D. F., Knight, G. A. and Nelson, W. A. 1999. Species recognition in New Zealand *Porphyra* using 18rDNA sequencing. *J. Appl. Phycol.* **11**: 421–8.
- Cole, K. M. 1990. Chromosomes. In Cole, K. M. and Sheath, R. G. (Eds) *Biology of Red Algae*. Cambridge University Press, New York, pp. 73–101.
- Coll, J. and Cox, J. 1977. The genus *Porphyra* C. Ag. (Rhodophyta, Bangiales) in the American North Atlantic. I. New species from North Carolina. *Bot. Mar.* **20**: 155–9.
- Coll, J. and Oliveira, E. C. 1976. The genus *Porphyra* C. Agardh (Rhodophyta, Bangiales) in the American South Atlantic. II. Uruguayan species. *Bot. Mar.* **19**: 191–96.
- Coll, J. and Oliveira, E. C. 1977a. Chromosome counting on 79-year-old-dried seaweed *Porphyra leucosticta* (Rhodophyta). *Experientia* **33**: 102.

- Coll, J. and Oliveira, E. C. 1977b. The nuclear state of 'reproductive' cells of *Porphyra leucosticta* Thuret in Le Jolis (Rhodophyta, Bangiales). *Phycologia* **16**: 227–9.
- Coll, J. and Oliveira, E. C. 1999. The benthic marine algae of Uruguay. *Bot. Mar.* **42**: 129–35.
- Conway, E., Mumford, T. F. Jr and Scagel, R. F. 1975. The genus *Porphyra* in British Columbia and Washington. *Syesis* **8**: 185–244.
- Dangeard, P. 1927. Recherches sur les *Bangia* et les *Porphyra*. *Botaniste* **18**: 183–244.
- Drew, K. M. 1954. Studies in the Bangioideae. III: Life-history of *Porphyra umbilicalis* (L.) Ktz. var. *Laciniata* (Lightf.) J. Ag. *Ann. Bot. N.S.* **18**: 183–211.
- Drew, K. M. 1956. Studies in the Bangiophycidae. *Bot. Rev.* **22**: 553–611.
- Dutcher, J. A. and Kapraun, D. F. 1994. Random amplified DNA (RAPD) identification of genetic variation in three species of *Porphyra* (Bangiales, Rhodophyta). *J. Appl. Phycol.* **6**: 267–73.
- Guiry, M. 1990. Sporangia and spores. In Cole, K. M. and Sheath, R. G. (Eds) *Biology of Red Algae*. Cambridge University Press, New York, pp. 347–76.
- Hamel, G. 1928. Notes d'algologie exotique. I. Sur quelques *Porphyra* des mers australs. *Ann. Cryp. Exot.* **1**: 51–7.
- Kapraun, D. F. and Freshwater, D. W. 1987. Karyological studies of five species of *Porphyra* (Bangiales, Rhodophyta) from North Atlantic and Mediterranean. *Phycologia* **26**: 82–7.
- Knight, G. A. and Nelson, W. A. 1999. An evaluation of characters obtained from life history studies for distinguishing New Zealand *Porphyra* species. *J. Appl. Phycol.* **11**: 411–19.
- Kornmann, P. 1994. Life histories of monostromatic *Porphyra* species as a basis for taxonomy and classification. *European J. Phycol.* **29**: 69–71.
- Kurogi, M. 1961. Species of cultivated *Porphyra* and their life histories (study of the life history of *Porphyra* II). *Bull. Tohoku Reg. Fish. Res. Lab.* **18**: 1–115.
- Kützing, F. T. 1843. *Phycologia generalis* F. A. Brockhaus, Leipzig, xxxii + 458 pp., 80 pls.
- Lindstrom, S. C. 1993. Inter and intrapopulation genetic variation in species of *Porphyra* (Rhodophyta: Bangiales) from British Columbia and adjacent waters. *J. Appl. Phycol.* **5**: 53–62.
- Lindstrom, S. C. and Cole, K. M. 1992a. Relationships between some North Atlantic and North Pacific species of *Porphyra* (Bangiales, Rhodophyta): Evidence from isozymes, morphology and chromosomes. *Can. J. Bot.* **70**: 1355–63.
- Lindstrom, S. C. and Cole, K. M. 1992b. A revision of the species of *Porphyra* (Rhodophyta, Bangiales) occurring in British Columbia and adjacent waters. *Can. J. Bot.* **70**: 2066–75.
- Lindstrom, S. C. and Cole, K. M. 1992c. The *Porphyra lanceolata* and *Porphyra pseudolanceolata* (Bangiales, Rhodophyta) complex unmasked: Recognition of new species based on isozymes, morphology, chromosomes and distributions. *Phycologia* **31**: 431–8.
- Lindstrom, S. C. and Cole, K. M. 1993. The systematics of *Porphyra*: Character evolution in closely related species. *Hydrobiologia* **260/261**: 151–7.
- Magne, F. 1991. Classification and phylogeny in the lower Rhodophyta: A new proposal. *J. Phycol.* **27** (Suppl. 3): 46.
- Mizuno, E. R. 1998. Aspectos reprodutivos e ecológicos de *Porphyra* spp (Rhodophyta, Bangiales) no litoral sudeste brasileiro: estudos em cultivo e na natureza. PhD thesis, Universidade de S. Paulo, S. Paulo, Brazil, 76 pp.
- Müller, K. M., Sheath, R. G., Vis, M. L., Crease, T. J. and Cole, K. M. 1998. Biogeography and systematics of *Bangia* (Bangiales, Rhodophyta) based on the rubisco spacer, *rbcL* gene and 18S rRNA gene sequences and morphometric analyses. 1: North America. *Phycologia* **37**: 195–207.
- Nam-Gil, K. 1999. Culture studies of *Porphyra dentata* and *P. pseudolinearis* (Bangiales, Rhodophyta), two dioecious species from Korea. *Hydrobiologia* **398–399**: 127–35.
- Oliveira, E. C. and Coll, J. 1975. The genus *Porphyra* C. Ag. (Rhodophyta, Bangiales) in the American South Atlantic. I: Brazilian species. *Bot. Mar.* **18**: 191–7.
- Oliveira, M. C. 1993. Filogenia de *Porphyra* spp (Rhodophyta): Sequenciamento do gene nuclear para o RNA da subunidade pequena do ribossomo (rRNA 18s) e estudos morfológicos da fase Conchocelis. PhD Thesis, Universidade de S. Paulo, S. Paulo, Brazil, 160 pp.
- Oliveira, M. C., Kurniawan, J., Bird, C. J. et al. 1995. A preliminary investigation of the order Bangiales (Bangio-phycidae, Rhodophyta) based on sequences of nuclear small-subunit ribosomal RNA genes. *Phycol. Res.* **43**: 71–9.
- Piriz, M. L. 1981. A new species and a new record of *Porphyra* (Bangiales, Rhodophyta) from Argentina. *Bot. Mar.* **24**: 599–602.
- Radmer, R. J. 1996. Algal diversity and commercial algal products. *BioScience* **46**: 263–70.
- Stegenga, H., Bolton, J. J. and Anderson, R. J. 1997. Seaweeds of the South African west coast. *Contrib. Bolus Herb.* **18**: 1–655.
- Stiller, J. W. and Waaland, J. R. 1993. Molecular analysis reveals cryptic diversity in *Porphyra* (Rhodophyta). *J. Phycol.* **29**: 506–17.
- Yoneshigue, Y. 1985. Taxonomie et ecologie des algues marines dans la région de Cabo Frio. PhD Thesis, Université d'Aix-Marseille II, Marseille, France.
- Yoshida, T. 1997. The history and future prospects of systematics of Bangiaceae, Rhodophyta. *Nat. Hist. Res.* **3** (Special Issue): 1–4.
- Yoshida, T., Notoya, M., Kikuchi, N. and Miyata, M. 1997. Catalogue of species of *Porphyra* in the world, with special reference to the type locality and bibliography. *Nat. Hist. Res.* **3** (Special Issue): 5–18.

APPENDIX I

Identification key for the leafy phases of *Porphyra* spp. found in Brazil and Uruguay

1. Margin dentate2
1. Margin smooth.....4
 2. Blades strap-shaped, up to 20 cm long*Porphyra acanthophora* var. *brasiliensis*
 2. Blades not strap-shaped, up to 9 cm long.....3
3. Plants forming rosulate tufts, texture membranaceous, but firm, barely adhering to paper, 16 (–32) carpospores and 64 spermatia per mother cell.....*Porphyra acanthophora* var. *acanthophora*
3. Plants not forming rosulate tufts, texture delicate, adhering well to paper, with 32 carpospores and 128 spermatia per mother cell*Porphyra pujalsiae*
 4. With monospores, spermatangia in pale elongated patches, not mixed with carposporangia.....*Porphyra leucosticta*
 4. Without monospores, spermatangia and carposporangia intermixed in a marginal and submarginal band.....5
5. Blades 0.1–0.5 cm wide, up to 10 cm long, twisted and with strongly folded margins*Porphyra spiralis* var. *spiralis*
5. Blades 1–14 cm wide, longer than 10 cm, not twisted or with strongly folded margins.....6
 6. Blades 1–5 cm wide, strap-shaped, with 64 spermatia per mother cell*Porphyra spiralis* var. *amplifolia*
 6. Blades more than 5 cm wide (usually 10 cm wide or more), with 16 or 128 (–256) spermatia per mother cell.....7
7. Blades up to 20 cm long, with 32 carpospores and 128 (–256) spermatia per mother cell*Porphyra rizzinii*
7. Blades up to 14 cm long, with 8 (–16) carpospores and 16 spermatia per mother cell*Porphyra drewiana*